On the Identity of *Murex triqueter* Born

(Gastropoda : Muricidae)

BY

EMILY H. VOKES

Tulane University, New Orleans, Louisiana 70118

(1 Plate; 2 Text figures)

It was first called to my attention by Anthony D'Attilio of the San Diego Natural History Museum that there were 2 Indo-Pacific species being identified as *Murex triqueter* Born, 1778. Mr. D'Attilio sent me the radula drawing reproduced here (Figure 4) and noted (*in litt.*) "This

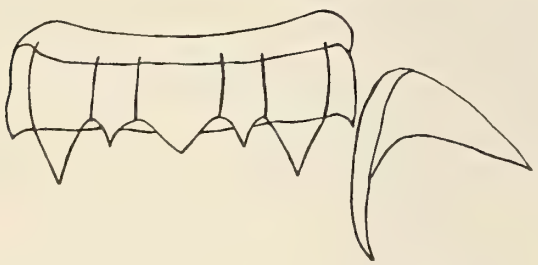

Figure 4

Chicoreus (Naquetia) triqueter (Born, 1778)
Drawing of radula by Anthony D'Attilio

radula doesn't look quite like the one figured by Cernohorsky [reproduced here, Figure 5], Veliger, v. 10, no. 2,

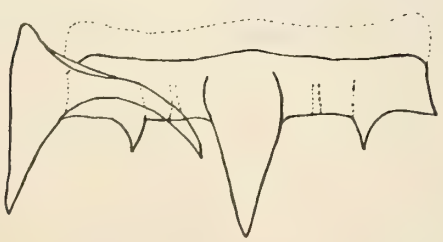

Figure 5

Chicoreus (Naquetia) trigonulus (Lamarck, 1816)
Drawing of radula after Cernohorsky, 1967, text figure 6

p. 125, fig. 6, shell on plt. 15, fig. 15. It is my idea from having studied *triqueter* that there is another very similar though distinct species. The two sometimes occupy the same geographic range but at times do not, or if they do the one species is more common. In the Indian Ocean and East Africa the true *triqueter* is very common, though the other species turns up rarely. In the South Pacific, *i. e.*, Queensland, Fijis, Solomons, the other is the commonly occurring species. In the Philippines both forms occur also, although I have the impression that *triqueter* is less common. Both also occur in Okinawa. Do you know of a name for the other species?"

Subsequent investigation indicated that his assessment was correct and also revealed an undue amount of confusion between the 2 forms. My questioning (Vokes, 1970: 184) of Cernohorsky's (1967: 124) identification of a Fijian shell as *Murex triqueter* led to his (Cernohorsky, 1971) figuring the type of certain other species involved, and greatly facilitated the ultimate resolution of the problem.

The morphological differences between the 2 species seem to be constant, although there is some intergrading. But, in general, it may be said that one of these species, which will be referred to as the "Indian Ocean form," is characterized by a marked roughness of shell texture with the varical flange noticeably squamose, this latter being the most easily observed difference in the 2 species. The color tends to be darker, with often an overall brown color rather than the maculated appearance of the other species. The second, which will be called the "Pacific form," has a smoother shell, marked by a cancellate sculpture composed of distinct spiral cords, crossed by narrow axial ridges. Where the axial ridges meet the sutures there are peculiar buttress-like structures similar to those usually associated with the members of the genus *Aspella*. The varical flange is composed of a single lamina and is not squamose. The length of the body whorl in proportion to the height of the spire is much greater in the Pacific form,

being on the order of 2:1, while the Indian Ocean form is approximately 1.5:1. As a result of this factor the aperture of the Pacific species is more oval than is that of the Indian Ocean form. The operculum of the latter is a darker brown color. The most convincing difference, however, as noted by Mr. D'Attilio, is the different radulae possessed by the 2 species (compare Figures 4 and 5).

Both forms have been referred to *Murex triqueter* by various authors. Obviously one of them is *M. triqueter* and the other is not. There are several possible names, but first we must ascertain which is, in fact, the true *M. triqueter* and which is "the other."

The root of the problem lies in the original description of *Murex triqueter* by Born. Born published two works, the first in 1778, entitled *Index rerum naturalium Musei Caesarei Vindobonensis.* In this work he listed a number of species, some of which were Linnaean and others which were new. The new species are not illustrated but, as was the custom of the times, bear references to previous illustrations in various iconographies. For his new species *Murex triqueter* there is a reference to Martini's *Conchylien-Cabinet,* v. 3, fig. 1038, a shell there denominated as "Purpura subalata, triquetra, variegata" and stated to be from the East Indies and Tranquebar. The shell, illustrated, unfortunately, only from the dorsal side, is the Indian Ocean species.

In 1780 Born published a second work entitled *Testacea Musei Caesarei Vindobonensis* and in this new edition he provided illustrations of his species based upon actual specimens in the Museum of the Kings of Vienna, now the Naturhistorisches Museum of Vienna. The specimens are still in the Museum and through the kindness of Dr. Oliver E. Paget I obtained a photograph of the specimen illustrated by Born. It is the Pacific species (see Figure *1*). Subsequent writers can scarcely be blamed if the 2 forms have been confounded. Most writers have resolved the dilemma by placing the 2 forms in synonymy, which does make everything much simpler. However, inasmuch as both Mr. D'Attilio and I, at least, are convinced that there are two distinct species involved, the question then becomes which of the two is *Murex triqueter* Born?

The question of whether a reference to a published figure is to take precedence over a "type specimen" is one that has bothered taxonomists for many years. The species of Linnaeus are particularly complicated in this fashion. Entire books have been written attempting to identify the Linnean species (*e. g.,* Hanley, 1855; Dodge, 1952 to 1959) but other early workers were little better. It was frequent to cite a previously published figure rather than to provide a new one because of the added expense of the engravings, if nothing else. In the case of Linnaeus often there are 3 or 4 references to as many species (sometimes genera) and establishing exactly which of these is to bear the name is difficult. When there is a single reference the problem is less complicated. But, nevertheless, specimens often have appeared later that are considered as part of the original type lot of the writer in question and frequently these do not agree with the figure that was the original reference for the species. In such a case what are we to do?

I once raised just this question before the International Commission on Zoological Nomenclature in connection with another species, and was told by Margaret Spillane (*in litt.*): "The type series includes previously published figures (Art. 73c(i)) and the specimens represented by such figures may be designated as lectotypes (Art. 74b). Does this not answer your query?" Article 73c(i) of the Code cited by Miss Spillane reads: "Syntypes may include . . . specimens not seen by the author but which were the bases of previously published descriptions upon which he founded his taxon in whole or in part." Article 74b adds that "Designation of a figure as a lectotype is to be treated as designation of the specimen represented by the figure; if that specimen is one of the syntypes, the designation as lectotype is valid from the nomenclatural standpoint." Therefore it is completely valid and legal to designate the specimen represented by the figure in Martini, v. 3, fig. 1038, a specimen stated to have been in the collection of Martini at the time, although I do not know where it presently resides, as the lectotype of *Murex triqueter.* The presence of a specimen in the Vienna Museum that is of a different species in no way countermands this selection for both the figure and the specimen are syntypes and, as such, both were equally available to be selected as lectotype. Had the Museum specimen been figured at the same time as the reference to the Martini figure, I would have suggested selecting the specimen, but in view of the 2 year's difference in the 2 publications it would seem that the figure has "priority." It is most probable that Born, as have many others later, considered the 2 forms as the same species, and hence it becomes a matter of restricting the name *M. triqueter* to one form or the other. I here select the first, with the type locality Tranquebar, as stated by Martini.

If there were any solid agreement among subsequent authors as to which form were to bear the name *triqueter,* I would have also been influenced by this factor. But certainly this is not the case. Röding (1798), interestingly, seems to have realized very early that there were 2 species involved. These he named *"Purpura" variegata* and *"Purpura" cancellata.* There is no doubt that he was attempting to distinguish between the 2 forms under discussion, as he cites *P. variegata* (in German) as the "checkered purple-snail," and *cancellata* as the "cancellate purple-snail."

Unfortunately he had only the single Martini figure for reference and so he employed it for both species, not anticipating the restrictions of latter-day nomenclators, and thus both of his names are objective synonyms of *Murex triqueter.*

Perry (1811), who recognized the previous species of no authors (although many of his species carry Linnaeus and Gmelin names), gave the Indian Ocean form a new name, *Triplex flexuosa,* with the locality as "New Zealand," a slightly erroneous assignment. Were the type of *Murex triqueter* picked to be the thin-flanged Pacific form, this name would be the first available for the Indian Ocean species.

In 1816 Lamarck published the illustrations of the *Encyclopédie Méthodique* (as *Tableau Encyclopédique et Méthodique*), although the text was not to appear for many years. However, there was a list of names accompanying the plates and the species figured therein date from "La Liste," as it is known. In this work we find a new species, *Murex trigonulus* Lamarck, that enters into our discussion. The ramifications of the identity of this species have been discussed in a previous work (Vokes, 1968a) but it will be necessary to repeat some of the data to make the entire history of *M. triqueter* intelligible.

Briefly, in 1816 Lamarck figured 2 species, one of which (plt. 417, fig. 1), cited as "*Murex triqueter* Born," is actually a specimen of the Caribbean *Chicoreus (Siratus) consuela* (Verrill, 1950), better known by the preoccupied name *Murex pulcher* Adams. The second species (plt. 417, fig. 4) Lamarck named *Murex trigonulus.* In 1822, Lamarck decided he was in error and placed the 1816 figure of his *M. trigonulus* in synonymy with *M. triqueter,* changing the other species (*i. e.,* the one that he had originally called *triqueter*) to a "variety b" of *M. triqueter.*

For some unknown reason Kiener, in 1842, chose to return to the 1816 designations rather than to employ the 1822 corrections and thus we find "*M. triqueter*" (plt. 40, fig. 3) is a fine example of *Chicoreus consuela,* and "*M. trigonulus*" (plt. 25, fig. 2) is the Indian Ocean species under discussion. In view of the fact that Cernohorsky (1971, fig. 3) has recently figured one of the syntypes of Lamarck's *M. trigonulus*[1] we now know what species originally was considered as *M. trigonulus* by Lamarck, although not by Kiener. The 1816 Lamarck illustration is somewhat ambiguous but it does emphasize the spiral cords that are characteristic of the Pacific species, whereas it is the axial ridges that are more pronounced in the Indian Ocean form. Deshayes (1832: 901), who finally published the text of the *Encyclopédie,* notes that Lamarck's plate 417, figure 4, "*Murex trigonatus*" (just to add further to the confusion) is a synonym of *M. triqueter.* From his description there is no doubt that Deshayes is describing the Indian Ocean shell, as he states that the last varix "est dilatée en aile assez mince et profondément plissée. Les plis sont écailleux en dessous." As in the case of Born, Lamarck probably had specimens of both species, and undoubtedly in the collections of the Paris Museum, studied by Kiener, there were both forms. Clearly Lamarck thought both were the same when he placed his *trigonulus* into synonymy with *triqueter.*

In 1822, Lamarck considering that the name *Murex trigonulus* was no longer being used, and was therefore free, reemployed it for another species, and it is this one that is frequently cited by authors as "*Murex trigonulus* Lamarck." I have discussed the identity of this species (Vokes, 1968a) and concluded that the species in question is that one later named *Pterynotus annandalei* Preston, 1910.

Cernohorsky's figuring of the specimen in the Muséum d'Histoire Naturelle, Geneva, no. 1099/35, as the only extant syntype and presumably, therefore, lectotype of the species has the effect of restricting the name *Murex trigonulus* Lamarck to the Pacific species. It was this selection in a large measure that influenced my subsequent

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[1] During the process of attempting to resolve the problem of identities the following information was sent from Dr. E. Binder, of the Muséum d'Histoire Naturelle, Geneva, to Dr. William K. Emerson, American Museum of Natural History, New York (1962, *in litt.*):

> "I send you two photographs of the possible type of Lamarck's *Murex trigonulus.* It was in Lamarck's collection, labeled '*M. triqueter* Born var.', but this may be a 'rectification' by a subsequent curator. I think it is the specimen figured in the Encyclopédie Méthodique Pl. 417, fig. 4 a&b. Its length is 38 mm; Lamarck indicates 18 lignes = 40½ mm.
>
> "If there had been any specimens in Lamarck's collection clearly labeled '*Murex trigonulus*', I would have had no trouble in finding out which was the Type. But there are no specimens so labeled.
>
> "Since Lamarck considered all his specimens figured in Encyclopédie Pl. 417 fig. 1 a&b and fig. 4 a&b as one and the same species, and they are certainly not *M. triqueter* Born, he must have made an error somewhere. It seems logical to think that these specimens might possibly be what Lamarck had first called *M. trigonulus,* and that by a later mistake he has attributed them to *M. triqueter.* This suspicion is reinforced by the fact that Kiener, who worked on Lamarck's collection, inverted both species.
>
> "I think this is the most likely definition one can give of *M. trigonulus,* but of course you do not have to adopt it."

This would seem to confirm the writer's opinion that Lamarck somehow changed his mind over the identity of his *Murex trigonulus* between 1816 and 1822. However, this would not affect the identity of the species originally given the name, once figured the species so named was committed to posterity for better or for worse.

selection of the Indian Ocean form to bear the name *Murex triqueter.* Thus both forms are well-established and the only remaining problem is to sort out the subsequent synonymy of the 2 species involved.

At the end of this paper I have a synonymic list for each of the 2 species; however, it should be noted that the references included are only those that have figures, or are otherwise clearly one form or the other. Simple citations of *"M. triqueter"* or *"M. trigonulus,"* without means of determining definitely which form is under consideration, are omitted.

As noted above, many writers, both early and late, have considered the 2 forms to be one species. Reeve, in the *Conchologica Iconica* (1845) was the first author to give a good figure of *Murex triqueter* under that name (plt. 1, fig. 4), noting "The *Murices triqueter* and *trigonulus* are figured in the 'Encyclopédie Méthodique' and in Kiener's 'Icon. Coq. Viv.' one for the other, and *vice versa.*" Accordingly, he figured as *"M. trigonulus"* a magnificent specimen of *Chicoreus consuela* (plt. 22, fig. 17).

A. Adams may have been the first to realize that there were 2 species involved for he named *Murex cumingii,* which he stated was "somewhat closely allied with the *M. triquetra* of Born" (1853: 270), and in his description he emphasizes "labro . . . fimbriato, fimbriis non squamulosis." In 1879, Sowerby, in the *Thesaurus Conchyliorum,* gave a good illustration of the Indian Ocean *M. triqueter* (fig. 114) and also a "variety *cumingii*" (fig. 115), indicating that he recognized a difference. Cernohorsky (1971, fig. 4) has also figured the lectotype of *M. cumingii* and it is obviously the same as *M. trigonulus,* named as new by Adams no doubt because of the confusion of true *M. trigonulus* with *M. triqueter.*

Tapparone-Canefri in his study of the mollusks of Mauritius (1881) compared *Murex cumingii* with *M. triqueter* and concluded that the 2 could be separated: "1° par sa forme générale . . . la spire [of *M. cumingii*] est plus courte relativement au dernier tour, l'ouverture est également plus grande et de forme ovale-allongée et non arrondie; 2° par la forme et la texture des varices, qui ne sont point saillantes et pas du tout épineuses; 3° par la coloration, qui est assez différente."

Among modern workers Habe seems to be the only one who has correctly identified these 2 species. Initially, in the Japanese edition of *Coloured Illustrations of the Shells of Japan* (II) Habe (1961) figured the Pacific species under the name *Naquetia triqueter* (plt. 25, fig. 13) but in the later English edition (Habe, 1964) of the work, entitled *Shells of the Western Pacific in Colour,* v. 2, he changed the identification to *Naquetia trigonalis* (Lamarck) [sic], and in 1966 Habe & Kosuge, in *Shells of the World in Colour,* v. 2, *The Tropical Pacific,* figured an example of the Indian Ocean shell, as *Naquetia triqueter* (p. 56; plt. 20, fig. 15), noting that the species is widely distributed south of the Philippines and in the Indian Ocean. They add that, although it resembles *N. trigonulus,* it may be clearly distinguished by the brown axial ridges.

There is another species, described from the Philippines by Sowerby, that may be a synonym of *Murex trigonulus.* This is *M. roseotinctus,* which Sowerby (1860: 429) described as "resembling *M. trigonulus* but wanting the expanded fringe at the lower part of the fronds of that species." The color is a beautiful pink, and in general shape the shell seems closer to the *Pterynotus annandalei* mentioned above, which to Sowerby was *"M. trigonulus,"* than to the true *M. trigonulus.* The species, which has not been recognized since its description, most nearly resembles the Caribbean *Chicoreus (Siratus) consuela,* suggesting possible mistaken locality data.

I would like to state that I too have been as confused as any by these 2 forms and in 1968 I figured a specimen of *Murex trigonulus* as *M. triqueter* (Vokes, 1968a: plt. 13, figs. 3, 4), because I did not realize that there were 2 species involved. When Mr. D'Attilio first raised the question of "What is the name for the other?" I began to investigate, and, from the distribution data, plus the fact that Cernohorsky (1967: p. 124) had placed *M. triqueter* var. *amanuensis* Couturier, 1907, in synonymy with the species he figured as *"M. triqueter"* (*ibid.,* plt. 15, fig. 15), which was the Pacific form, and from Couturier's statement that his Tahitian shell differed from the type by the more slender and elongated anterior canal, I came to the conclusion that *amanuensis* was the first available name for the Pacific form, believing erroneously that *M. trigonulus* was the same form as *M. triqueter* (having been led astray by Kiener and Deshayes, as well as Lamarck).

Murex triqueter Born was named as the type of the genus *Naquetia* Jousseaume, 1880. Regardless of which form is taken to be the true *N. triqueter,* the generic concept is not changed. I have previously considered *Naquetia* to be a subgenus of *Pterynotus,* but in the course of preparing the present paper, I have come to realize that *Naquetia* is more closely allied with *Chicoreus.* My reason for this change of opinion is that I had the opportunity to see a juvenile specimen of *N. triqueter* and from the nature of the early development it is obviously of the *Chicoreus* group rather than the *Pterynotus* group. I have discussed these 2 basic lineages of Muricidae in other papers (*e. g.,* Vokes, 1968b: 86) and it can be seen that there are two very fundamental types of early development observed in the Muricinae. One of these is the type found in the *Pterynotus-Poirieria* line where, on the first post-nuclear whorl, there are 6 small fin-like

varices. In *Pterynotus* every other one of these disappears on the second or third teleoconch whorl, leaving 3 varices and 3 intervarical nodes per whorl. In *Poirieria, Paziella,* etc., these 6 varices simply persist to the adult stage. But in the *Hexaplex-Chicoreus-Murex s. s.* lineage the early development is totally different. On the first post-nuclear whorl there are 12 small axial ribs, and on succeeding whorls certain of these change into small spinose or foliaceous varices, 3, 4, 6, or more to a whorl, with the others remaining as intervarical nodes. The juvenile *N. triqueter* has this latter type of development with, on the second teleoconch whorl, every 4th rib becoming a varix and the intervening 3 becoming intervarical nodes. This pattern persists up to the adult stage. Furthermore, the young *N. triqueter* has spines on the shoulder and on the siphonal canal, as seen in *Chicoreus.*

The second factor that influenced my change of generic assignment is the nature of several allied species, in particular, *"Murex" laciniatus* Sowerby, which usually appears to be a *Chicoreus* but in extreme individuals may develop an expanded wing-like flange on the anterior canal that looks exactly like *Naquetia.* Certain other members of *Naquetia,* especially *"Pterynotus" annandalei,* tend to merge with the members of the subgenus *Chicoreus (Siratus),* but in the latter group there is no varical flange along the anterior canal, which is usually greatly extended. Thus the species *"Murex" superbus* Sowerby, 1889, and *"Murex" consuela* Verrill are assigned to *Siratus,* in spite of a marked affinity to *"M." trigonulus* and *"P." annandalei,* because they have spines on the siphonal canal rather than a flange.

I am of the opinion that the different lineages of *Chicoreus, i.e., Phyllonotus,* and *Siratus,* and now *Naquetia,* are all probably more closely related to each other than they are to *Chicoreus.* Again we are confronted with the familiar problem of the oldest generic name not necessarily being the oldest morphotype. In the early stages of evolution *Phyllonotus* and *Chicoreus* are much more closely akin than are the modern forms. The morphotype that has been given the name *Torvamurex* (type: *Triplex denudatus* Perry) is the more normal "ancestral" *Chicoreus,* and its relationship to the other subgenera is more obvious than the *Chicoreus* typefied by *C. ramosus* with its elaborate frondose varices.

The geologic history of these various lines is not completely known but all indications at present are that in the New World *Phyllonotus* was derived from a *Hexaplex* ancestor during the Oligocene, and *Siratus,* in turn, developed from a *Phyllonotus* ancestor. At the same time *Chicoreus s.s.* was also being derived, and as there are no members of *Phyllonotus* known from the central European area where the oldest *Chicoreus* appears, in all probability *Chicoreus* and *Phyllonotus* represent parallel but separate diversions. The oldest known *Chicoreus s.s.* (*Murex nudus* Noszky) is from the Oligocene of Hungary and looks very little different from the earliest *Phyllonotus.* However, in the Miocene of the European region the line develops into true *Chicoreus* and in the New World it develops into *Phyllonotus.* If the modern species of *Phyllonotus* were not so distinctive, the early members would be just as easily placed in *Chicoreus s.s.*

The species I have considered to be the ancestral *Naquetia, "Murex" williamsi* Sokolov, is totally different from this *Phyllonotus*-like form and evidently represents a distinct line of evolution. (It is entirely possible that the resemblance between *"Murex" williamsi* and *"Murex" trigonulus* is coincidental and this species from the Upper Eocene of Ukrainia is not actually related to the *Naquetia* line.) Unfortunately nothing is known of the nature of the early whorls of this fossil species, but the cancellate ornamentation suggests that the early whorls are like those of the other *Naquetia* species. If this species is, in fact, the progenitor of the *Naquetia* line, in all probability the species of *Chicoreus (Siratus)* seen in the Pacific region are separately derived from this line and are not closely related to the western Atlantic species of *Siratus.* The phylogenetic development of these groups would seem to give credence to the statement often made that there is no such thing as a "phylogenetic tree" but rather we have phylogenetic "reticula" or nets. It would appear that *Na-*

Explanation of Figures *1* to *3*

Figure *1*: *Murex triqueter* Born, 1778. Syntype, Naturhistorisches Museum, Vienna, no. NHMW 76.566. Height 53.1 mm, diameter 22.0 mm (× 1½, approximately). Photograph courtesy Dr. Oliver E. Paget, Naturhistorisches Museum, Wien.

Figure *2*: *Chicoreus (Naquetia) triqueter* (Born, 1778). Hypotype. Height 70.0 mm, diameter 29.0 mm (× 1½). Rabaul, New Britain.

Figure *3*: *Chicoreus (Naquetia) trigonulus* (Lamarck, 1816). Hypotype. Height 60.0 mm, diameter 27.3 mm (× 1½). Guam, Mariana Islands.

Figure *1*a

Figure *1*b

Figure *2*

Figure *3*